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Habitat Use and Behavior of the East Pacific Green Turtle, *Chelonia mydas*, in an Urbanized System

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Abstract.—Green sea turtles, *Chelonia mydas*, are known to inhabit populated and often urbanized areas. To understand turtle habitat use and behavior within these unique habitats, seven juvenile green turtles were fitted with acoustic transmitters (September 2012 – August 2014), of which two transmitters included an accelerometer (AP transmitter). One individual fitted with an AP transmitter was tracked using a passive acoustic array in an urbanized river, the San Gabriel River, Long Beach, CA (33°45' N, 118°05' W). Three additional turtles in this river and three turtles (one with AP transmitter) in a restored estuary (33°44' N, 118°03' W) in southern California were actively tracked for two non-consecutive 24-h periods. Those fitted with AP transmitters indicated that turtles were less active at night (0.58 $\pm$ 0.56 m/s^2 and 0.50 $\pm$ 0.63 m/s^2) than during the day (0.86 $\pm$ 0.63 m/s^2 and 0.78 $\pm$ 0.60 m/s^2) at both sites. Activity data and corresponding movements of the actively tracked turtle fitted with the AP transmitter were used to infer resting periods for other tracked individuals. Turtles rested near bridge pilings and runoff outflows in the river to potentially shelter from tidal flow. Turtles used significantly larger daily areas in the urbanized river (0.046 $\pm$ 0.023 km^2) where resources may be patchier and less abundant, compared to turtles in the estuary (0.024 $\pm$ 0.012 km^2) where large, dense eelgrass beds are present. Based on the habitat use and behaviors of green sea turtles, it appears that some green sea turtles are able to make use of both highly developed and restored habitats and likely benefit from certain aspects of development.

Green sea turtles, *Chelonia mydas*, have been listed and protected in the United States under the Endangered Species Act (ESA) since 1978 (FWS and NMFS, 80 FR 15271). Through decades of research and assessment programs, populations have increased throughout different areas of the world (Chaloupka and Limpus 2001, Godley et al. 2001, Balazs and Chaloupka 2004). Specifically, the east Pacific green sea turtle (hereafter referred to as green turtle) population has shown signs of recovery through an increase in nesting females in Michoacán, Mexico (largest nesting aggregation in the population), likely a result of nesting beach protection in 1979 in Mexico coupled with a reduction in poaching in foraging areas (Seminoff et al. 2015).

As this green turtle population continues to increase, we expect turtle abundance to increase at the edges of their range and new individuals to expand the population range as far as their thermal tolerance will allow. Currently, the northern residential limit of this population is the heavily urbanized region of southern California. In California, roughly 90% of the natural wetlands and riparian habitat have been destroyed or altered in some way (Allen and Feddema 1996, Smith 1999, Ackerman and Stein 2007). Adult green turtles use these types of coastal habitats to forage, while juveniles use them for up to 20 years where they feed on various species of algae, eelgrasses, and invertebrates until they reach maturity at approximately 30 years of age (Musick and Limpus 1997, Seminoff et al. 2002b, Goshe et al. 2010). Therefore, due to the reduction of natural suitable habitat, individuals may seek out these urbanized estuarine environments in search of food and refuge. However, few studies have investigated how green turtles use these types of urban habitats (Renaud et al. 1995, MacDonald et al. 2012, MacDonald et al. 2013).

Anecdotal evidence suggested that an unknown number of green turtles have been observed within anthropogenically-altered habitats further north of their previously known residential range within the east Pacific (San Diego Bay, CA) at Long Beach and Seal Beach, CA for at least the last 50 years in smaller numbers (D. Lawson, pers. comm.). This aggregation of green turtles seems to have increased (D. Lawson, pers. comm.) and primarily been observed inhabiting the San Gabriel River, a highly urbanized river that is channelized with rocky levees and lined with two electric generating plants (herein referred to as "power plants"). Despite this increase in green turtle presence, the river lacks eelgrass (Merkel & Associates Unpub. data), which is a major green turtle food source. In addition, green turtles have been found in the more "natural" Seal Beach National Wildlife Refuge (SBNWR) composed of some restored habitat, including shallow saltwater basins and tidal channels that were dredged out as part of restoration project. Specifically, green turtles have been observed within a smaller eelgrass covered, recently restored, dredged saltwater basin called the 7^{th} St. Basin (Jirik and Lowe 2012).

Further, previous passive acoustic telemetry monitoring has indicated that juvenile green turtles likely remain in the river year around, while some individuals spend the warmer months in the basin (Crear et al. 2016); however, based on the low positional accuracy (50 – 600 m) of passive tracking it is unclear how green turtles are selecting for microhabitats within these altered environments. As a result of the anthropogenic changes made to coastal habitats, we expect to see a change in prey density and an influence in foraging habitat use, which should in turn, directly influence green turtle area use and habitat selection. For example, in the San Gabriel River green turtles have to rely on prey items like algae and invertebrates because the river lacks eelgrass. As a result of this missing resource, green turtles might be expected to use more of the river in search of prey compared to a habitat that has an abundance of eelgrass (e.g. SBNWR) (Whiting and Miller 1998, Seminoff et al. 2002a, Makowski et al. 2006, Seminoff and Jones 2006). Individuals in altered areas may also undergo behaviors that are often observed in natural habitats, like displaying higher activity levels during the day (possibly foraging) (Heithaus et al. 2002, Makowski et al. 2006, Blumenthal et al. 2010). Green turtles may also adapt to the presence of various manmade hard structures (i.e. rocky levees) by resting, a behavior that has been observed along natural vertical features to avoid predation and tidal currents (Shaver 1994, Makowski et al. 2006, Seminoff et al. 2006). These behaviors have not been addressed in green turtles that inhabit urbanized habitats.

These study sites present a unique opportunity to understand how green turtles use habitats in a heavily urbanized environment (the San Gabriel River) compared to an adjacent, restored, more "natural" environment (SBNWR). Based on diel differences in habitat use and movements of green turtles and the differences between the two sites, it was hypothesized that green turtles would: 1) use smaller activity spaces, move shorter distances, and travel more slowly within the smaller, eelgrass-covered 7^{th} St. Basin, 2) exhibit more resting behavior at night by moving less at both sites, and 3) display a behavior indicative of resting while associating with hard structures within the river at night. Understanding how a recovering threatened species behaves in an altered environment compared to a restored one will inform management as to the best habitats to protect or restore, ensuring populations continue to increase.

Materials and Methods

The San Gabriel River (33°45' N, 118°05' W; estuarine region) is a highly urbanized river, lined with concrete and channelized near the mouth (Stein 2007), that discharges into the Pacific Ocean between Long Beach, CA and Seal Beach, CA (O'Brien et al. 2011). The concrete portion extends from upriver to approximately six km upstream from the mouth of the river (i.e. green turtles cannot access upstream of six km from the mouth of the river because the river is lined by concrete and too shallow). Where the concrete portion ends, depth increases to approximately four meters, providing 0.51 km^2 of estuarine river habitat (Fig. 1). The substrata along this stretch of river consists of mostly fine sediments; however, hard structures like rocky levees and runoff outflows from the two power plant systems line either side (Merkel & Associates Unpub. data). This highly urbanized river supports multiple species of fish, mollusks, arthropods, polychaetes, and marine algae either as infauna within the muddy substratum or as epifauna among the hard structures (Turner and Strachan 1969). Many of these species often serve as prey for juvenile green turtles (Blumenthal et al. 2010, Carrión-Cortez et al. 2010). Although there is a diverse benthic community in the San Gabriel River, there are no eelgrass beds (Merkel & Associates Unpub. data), which are thought to be an important food source and common habitat component in some areas where green turtles forage (Musick and Limpus 1997).

Unlike the highly urbanized San Gabriel River, the SBNWR (33°44' N, 118°03' W) is a 14-km^2 estuary surrounded by the Seal Beach Naval Weapons Station and is inaccessible to the public (Fig. 1). SBNWR has four restored dredged estuarine basins which connect to Anaheim Bay through a network of dredged channels (Jirik and Lowe 2012) (Fig. 1). Green turtles have been observed in one of the restored basins (7^{th} Street Basin: 0.15 km^2; less than a third of the San Gabriel River) since 2008 (K. Jirik, pers. comm.). A concrete culvert (1.5 × 2.4 × 12.0 m) dampens tidal flow in and out of the 7^{th} St. Basin and animals are able to swim freely through the culvert except during strong tidal changes (Jirik and Lowe 2012). Depth is relatively uniform and shallow (<3 m) throughout the basin; therefore, water temperatures within the 7^{th} St. Basin get warmer than the adjacent natural estuary in the summer, but become colder in the winter (Jirik and Lowe 2012). In fact, green turtles have only been observed in the 7^{th} St. Basin during the warmer months (Crear et al. 2016; K. Gilligan, pers. comm.). A muddy substratum is uniformly distributed throughout the 7^{th} St. Basin; however, unlike the San Gabriel River, large patches of eelgrass (*Zostera marina* and *Enteromorpha* spp.) cover over 40% of the basin (Merkel & Associates Unpub. data).

Green turtles were caught using entanglement nets (set time: 1-5 hrs; checked nets < 30 mins; net length: 50-150 m; mesh size: 0.3 m) in the San Gabriel River and 7^{th} St. Basin approximately every three months from June 2012 to August 2014 (Fig. 1). When green turtles were caught, they were removed from the net, kept on the boat (San Gabriel River) or brought to shore (7^{th} St. Basin) for work up. Straight carapace length (SCL, ± 0.1 cm) was measured and each turtle was weighed (± 1.0 kg), tagged with an Inconel flipper tag (Style 681, National Band and Tag Company, KY), and injected with an internal passive integrative transponder (PIT) tag (Avid, Norco, CA). A subsample of individuals was fitted with a continuous acoustic transmitter (V13-1L, 13 × 45 mm, frequencies: 60-84 kHz, continuous pulse rate 2000 ms, power output: 153 dB, 12 g in air, VEMCO Ltd). Transmitters were attached to the carapace using a fiberglass cloth and resin laminate (Balazs et al. 1996). Upon completion, all turtles were released at the capture location within 1.5 hrs.

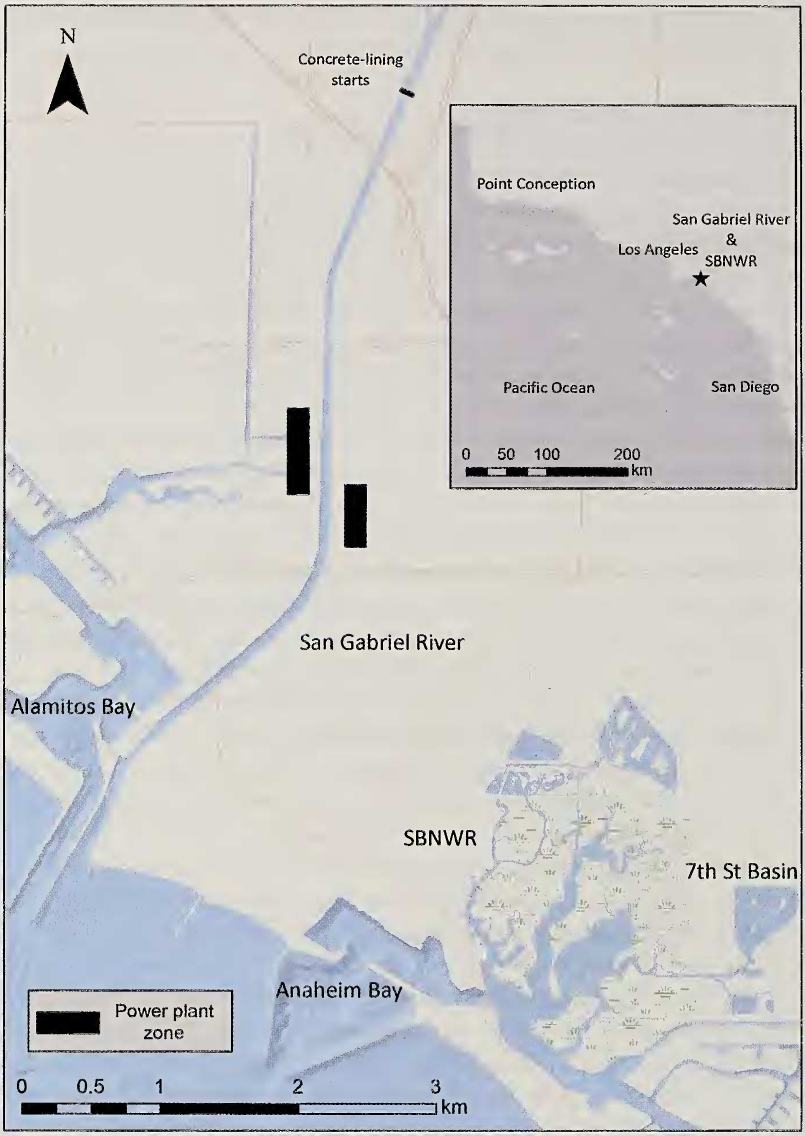

Fig. 1. Map of the San Gabriel River and 7th St. Basin within the Seal Beach National Wildlife Refuge (SBNWR). Concrete-lining begins at 6 km from the river mouth and continues upstream.

Tagged green turtles were actively tracked for two non-consecutive 24-h periods at least a day following capture and release in order to avoid behavioral changes due to capture stress. Individuals were tracked from a 4.3-m aluminum boat using a directional hydrophone (VH110, VEMCO Ltd, Bedford, Nova Scotia) and an acoustic tracking receiver (VR100, VEMCO Ltd). The VR100 records the gain, time, date, latitude and longitude, and signal strength of each detection. At 10 min intervals, VR100 positional data with the highest signal strength above 80 dBs under a gain of zero were selected for inclusion in the data set, except in areas where the attenuation of the transmitter's signal was altered due to the turbulence from the power plants discharged water. Due to this attenuation, if the turtle was in the discharge outflow all received signal strengths were kept. If a tracked turtle was detected moving into the power plant discharged outflow in the San Gabriel River and the signal was lost, a fixed position corresponding to the opening of the closest discharge station was recorded. All VR100 detections at 10-min intervals that followed the previous criteria were considered valid geolocations. Some intervals between geolocations were greater than 10 min due to the time required for replacing tracking personnel; therefore, the number of geolocations varied for each track.

Transmitters were range-tested to determine the distance the VR100 (at a gain of zero) must be from the transmitter on the turtle in order to get an accurate location of the turtle at various locations within the study sites. To do this, the researcher made several passes by a transmitter suspended midwater, while using the directional hydrophone and VR100 to measure signal strength. The range-test assessed the signal strength from 0-150 m away from multiple directions. The results of the range test indicated that the tracker would need to be within 10 m of the tagged turtle in order to receive a signal strength of 80 dB or higher; however, this distance significantly decreased in power plant discharge locations.

Accelerometer and pressure sensing (AP) coded acoustic transmitters were fitted to the carapace of two individuals to determine when turtles were resting. An AP transmitter initially transmits its unique ID and pressure value, then measures acceleration on three axes (X,Y,Z) at 5 Hz over a given time period (T), calculates the root mean squared (RMS; m/s^2) for the three axes, and then transmits the RMS value. This value represents the average acceleration over the three axes and the general activity index of the animal in this study (O'Toole et al. 2011). The shallow depth of both sites made it difficult to use any of the depth data provided by the AP transmitter. One of the two turtles fitted with an AP transmitter (V13AP-1L, 13 $\times$ 44 mm, frequencies: 69 kHz, pulse rate 15 s, T: 12 s, estimated battery life: 104 days, power output: 153 dB, 12.3 g in air, VEMCO Ltd) was included in the subsample of turtles actively tracked in the 7^{th} St. Basin, for which acceleration was acquired in real time via the VR100 with an associated signal strength. The second individual tagged with an AP transmitter (V13AP-1L, 13 $\times$ 44 mm, frequencies: 69 kHz, random pulse rate 40-80 s, T: 37 s, estimated battery life: 203 days, power output: 153 dB, 12.3 g in air, VEMCO Ltd) was detected and archived by a passive acoustic array from a concurrent study (15 VR2W acoustic receivers, VEMCO Ltd), in which receivers were spaced 300–600 m apart within the San Gabriel River from the river mouth to the concrete lined portion of the river (Crear et al. 2016). Horizontal movements of this individual were included in Crear et al. (2016), while this study incorporated only the individual's acceleration values.

Using the valid VR100 geolocation data every 10-min, localized convex hulls (LoCoHs) were created for each individual 24-h track to determine daily activity use and core area use in R (v. 3.2.3, R Core Team, 2015) using the adehabitatHR, adehabitatHS, fields, and maptools packages (Calenge 2006, Bivand and Lewin-Koh 2013, Furrer et al. 2013). LoCoHs were used due to their ability to handle geomorphological boundaries (e.g. river and estuary boundaries) when constructing utilization distributions (Getz and Wilmers 2004, Getz et al. 2007). Adaptive or a-LoCoH method was used in which a hull is constructed around each reference point and nearby points, where the sum of the distances between nearby points and the reference point equals a. The value of a is selected for each individual based on the distance that individual traveled during that track. The hulls are then merged together from smallest to largest (Getz et al. 2007). The area in which 95% of the hulls were merged represented green turtle daily area use, while the area in which 50% of the hulls were merged represented green turtle core area use. In order to take into account the differences in the number of geolocations acquired among tracks and possibility of autocorrelation, bootstrapping was done for each track, where only a subset of geolocations was randomly selected. Linear mixed effects models were used to compare daily and core area use sizes from each green turtle track between the two sites with turtle and individual track as random effects in the R package lme4 (Bates et al. 2013). Both core and daily area use sizes were log transformed in order to achieve equal variances. A likelihood ratio test was used to compare each model to the model without site. Core and daily area use LoCoHs from each track were mapped in ArcGIS 10.2.

To determine when periods of resting occurred, first passage time (FPT) was used. FPT is the time required for an animal to cross a circle of a given radius, where movements become more tortuous the longer it takes an animal to cross the circle (Fauchald and Tveraa 2003, Papastamatiou et al. 2012). This type of analysis is typically used to determine periods of area-restricted search (ARS); however, higher FPT values are indicative of resting; therefore, we referred to it as area-restricted-use (ARU). The circle radius or the spatial scale of ARU selected was 25 m for the analysis because it was thought that a turtle resting on the bottom, followed by the individual ascending to the surface for a breath, then descending back down to possibly a new area would not exceed a circle with a radius of 25 m. It is important to note that 25 m is greater than the errors in the geolocations, which ensured that we were analyzing turtle movements, not geolocation error. FPT analysis was conducted on each track for each individual using adehabitatLT package in R (Calenge 2006). To validate high periods of FPT corresponding with resting (ARU), a Pearson's product-moment correlation was conducted between FPT values from the actively tracked turtle fitted with an AP transmitter and the corresponding RMS acceleration values (see Results). Based on the relationship between RMS acceleration and FPT data and observations in the field, when an FPT value was greater than 4000 sec (67 mins), the turtle was assumed to be resting and undergoing ARU. Each point was assigned a "yes" or "no" for resting or not based on the FPT value at that point. This threshold was used on all tracked individuals in order to predict periods of resting. To determine whether turtles spent more time resting during the day or at night or between sites, a generalized linear mixed effects model with a binomial distribution was used with turtle as the random effect. A likelihood ratio test was then used to compare the full model to models without each factor (diel period and site).

To provide support for ARU and resting behavior results for different diel periods between sites, various movement metrics were quantified. The total distance traveled and rate of movement (ROM) were determined for day, night, and the complete track. Total distance traveled was determined by summing the distances between each subsequent 10 min geolocations. ROM was calculated as the distance traveled between two consecutive geolocations, divided by the time taken by the green turtle to swim between the two geolocations. Pearson's product-moment correlations were conducted to test for a negative correlation between all combined FPT and ROM values from the river tracks and all combined FPT and ROM values from the basin tracks. In addition, to determine if the distance traveled and ROM differed between day and night or between the two sites, linear mixed effects models were used with individual green turtle as a random effect in R v. 3.0.1 using the nlme package (Pinheiro et al. 2013). ROM values were $\log(x + 1)$ transformed in order to achieve equal variance. All statistics were evaluated at significance levels of $\alpha = 0.05$.

Substrate type and eelgrass presence or absence were characterized in both the San Gabriel River and the SBNWR using interferometric sidescan sonar with dual antenna differential GPS by Merkel & Associates (Unpub. data). Ground-truthing was completed at both sites using a combination of visual surveys from shore, snorkel, SCUBA, ROV, and drop camera verification (Merkel & Associates Unpub. data). Substrate type was divided into six groups in the San Gabriel River: non-vegetated soft bottom, mixed rubble/soft bottom, rubble/hard bottom, engineered structures (bridge pilings, cement discharge structures, runoff outflows), debris, and

Table 1. Summary of size, tracking duration and tracking location for the six green turtles tracked. Turtle 2 was fitted with an AP transmitter and actively tracked for nonconsecutive 24-hs periods. Turtle 7 was fitted with an AP transmitter and monitored by the acoustic array in the San Gabriel River for 69 days. SCL = straight carapace length; Duration of tracks = the combined hours of the two nonconsecutive tracks; SGR = San Gabriel River.

Turtle No.	SCL (cm)	Mass (kg)	Date Tagged	1st Track Date	2nd Track Date	Duration of Tracks (h)	Site Tagged/ Tracked
1	66.3	42	8-Aug-12	28-Sep-12	16-Nov-12	45	SGR
2	56.8	20	10-Jul-13	15-Jul-13	29-Jul-13	48	SBNWR
3	61.4	27	2-Feb-14	14-Feb-14	21-Mar-14	48	SGR
4	74.3	52	29-May-14	6-Jun-14	13-Jun-14	48	SGR
5	67.1	45	5-Aug-14	11-Aug-14	15-Aug-14	48	SBNWR
6	50.8	41	6-Aug-14	18-Aug-14	23-Aug-14	48	SBNWR
7	54.8	23	28-Aug-13	-	-	-	SGR

intertidal sand beach. Within the SBNWR, substrate types were divided up into vegetated and non-vegetated (Merkel & Associates Unpub. data).

To quantify habitat use, habitat selection index (HSI) was used to determine green turtle preference or avoidance of non-vegetated soft bottom, mixed rubble/soft bottom, hard rubble, engineered structures, debris, and intertidal sand beach in the San Gabriel River. Habitat selection index was also used to determine green turtle preference or avoidance of the culvert in the 7th St. Basin. A 100 m buffer was made around the culvert to indicate affinity to habitat around the culvert. The area near the culvert was separated into non-vegetated areas (culvert/non-vegetated) and eelgrass covered areas (culvert/eelgrass) based on the presence or absence of eelgrass. The area away from the culvert was also separated into non-vegetated areas (no culvert/non-vegetated) and eelgrass covered areas (no culvert/eelgrass). Based on the criteria determined in Topping et al. (2005), HSI was calculated by taking the percent of the individual's geolocations over a given habitat (habitat use) divided by the percent of each available habitat within the river or the basin (habitat availability). HSI values > 1 and < 1 indicate preference and avoidance, respectively, of a particular habitat type. HSI values were calculated for each habitat type for each turtle during the day, night, and 24-h period, as well as for periods when the turtle was assumed resting (determined through FPT analysis). Habitat selection was analyzed at each site using a chi-square test for each individual turtle. Once a chi-squared value was determined for each individual, chi-squared values were summed to get an overall chi-squared statistic. HSI were calculated in ArcGIS 10.2.

Results

Six juvenile green turtles were tracked for two nonconsecutive 24-h periods (three in the San Gabriel River and three in the 7th St. Basin) between September 2012 and August 2014 (Table 1). No green turtles left the San Gabriel River while they were tracked; however, one green turtle exited the 7th St. Basin through the culvert, but remained close to the basin and did not travel to any other area in SBNWR for the remainder of the study. The fewest geolocations for a track were 81; therefore, each LoCoH run was created using 81 randomly selected geolocations from each individual 24-h track. The difference in green turtle core area use (50%) was not significant (Likelihood-ratio test, $\chi 2 = 3.70$, $p = 0.055$) between the San Gabriel River and the 7th St. Basin at an $\alpha = 0.05$ due to the large variability among individuals. The mean for the river (mean $\pm$ SE) (11811 $\pm$ 270 m^2; Fig. 2 a-c) was over twice that for the 7th St. Basin (5113 $\pm$ 127 m^2; Fig. 2d). There was a significant difference in daily area use (95%) between the two

Table 2. Percent of time individuals rested during the day and night over each 24-hs track. Tracks where % Resting was 0 is indicative of the individual not exhibiting resting behavior. SGR = San Gabriel River

			% Resting	
Turtle #	Track	Location Tracked	Night	Day
1	1	SGR	100	2
1	2	SGR	69	37
2	1	7th St. Basin	28.6	21.7
2	2	7th St. Basin	73.2	1.5
3	1	SGR	53.7	25
3	2	SGR	15.2	42.9
4	1	SGR	0	0
4	2	SGR	0	0
5	1	7th St. Basin	0	3.3
5	2	7th St. Basin	20	11.9
6	1	7th St. Basin	0	0
6	2	7th St. Basin	24	0

sites (San Gabriel River: 46552 ± 943 m^2; 7th St. Basin: 23789 ± 539 m^2) (Likelihood-ratio test, $\chi 2 = 4.51$, $p = 0.034$). No overlap occurred among the locations of the core areas of individuals within the San Gabriel River (Fig. 2a-c). At the 7th St. Basin, Turtle 2 and Turtle 5 had a 2.5% overlap and Turtle 5 and Turtle 6 had a 21.7% overlap (Fig. 2.d). The locations of core areas between the two tracks of an individual varied as well, with five of six turtles showing no overlap in the core areas of their two tracks (Fig. 2a-d). Turtle 6 exhibited a small amount of overlap (19.6%) in core area between its two tracks in the 7th St. Basin (Fig. 2d).

Turtle 2, which was fitted with an AP transmitter and actively tracked twice within the 7th St. Basin showed a higher mean acceleration during the day (0.79 ± 0.015 m/s^2) compared to at night (0.47 ± 0.018 m/s^2) (Fig. 3a). Turtle 7, which was also tagged with an AP transmitter, was monitored and acceleration data was archived for 69 days by the passive acoustic array within the San Gabriel River (Crear et al. 2016). Mean acceleration for Turtle 7 in the river was higher during the day (0.86 ± 0.0074 m/s^2) compared to during the night (0.58 ± 0.0076 m/s^2). Further, the distribution of acceleration values differed between day and night with a high frequency of acceleration values from 0.0-0.1 m/s^2 at night and 0.4-1.0 m/s^2 during the day (Fig. 3b).

There was a significant negative correlation between FPT values and acceleration values (Pearson's product-moment correlation, $p < 0.05$; $r = -0.19$) for the turtle tracked in the 7th St. Basin for two 24-h periods (Fig. 3a). This result validated the relationship between high periods of FPT and resting (ARU). In addition, there was a significant negative correlation between FPT values and ROM values for all individuals in the river (Pearson's product-moment correlation, $p < 0.001$; $r = -0.36$) and 7th St. Basin (Pearson's product-moment correlation, $p < 0.001$; $r = -0.41$) (Fig. 4b,d). Based on the 4000 sec threshold, resting occurred on 75% of the tracks (Table 2). Turtles appeared to rest for a significantly greater proportion of time during the night (33.0%) compared to during the day (11.7%) ($\chi 2 = 82.50$, $p < 0.001$); however, there was no difference in the proportion of time spent resting between the two sites (Likelihood-ratio test, $\chi 2 = 0.0002$, $p = 0.99$).

All tracked turtles traveled further and had a higher mean ROM during the day than at night (ANOVA, $F_{1,17} = 30.16$, $p < 0.001$, $F_{1,1266} = 131.66$, $p < 0.001$); however, there was no

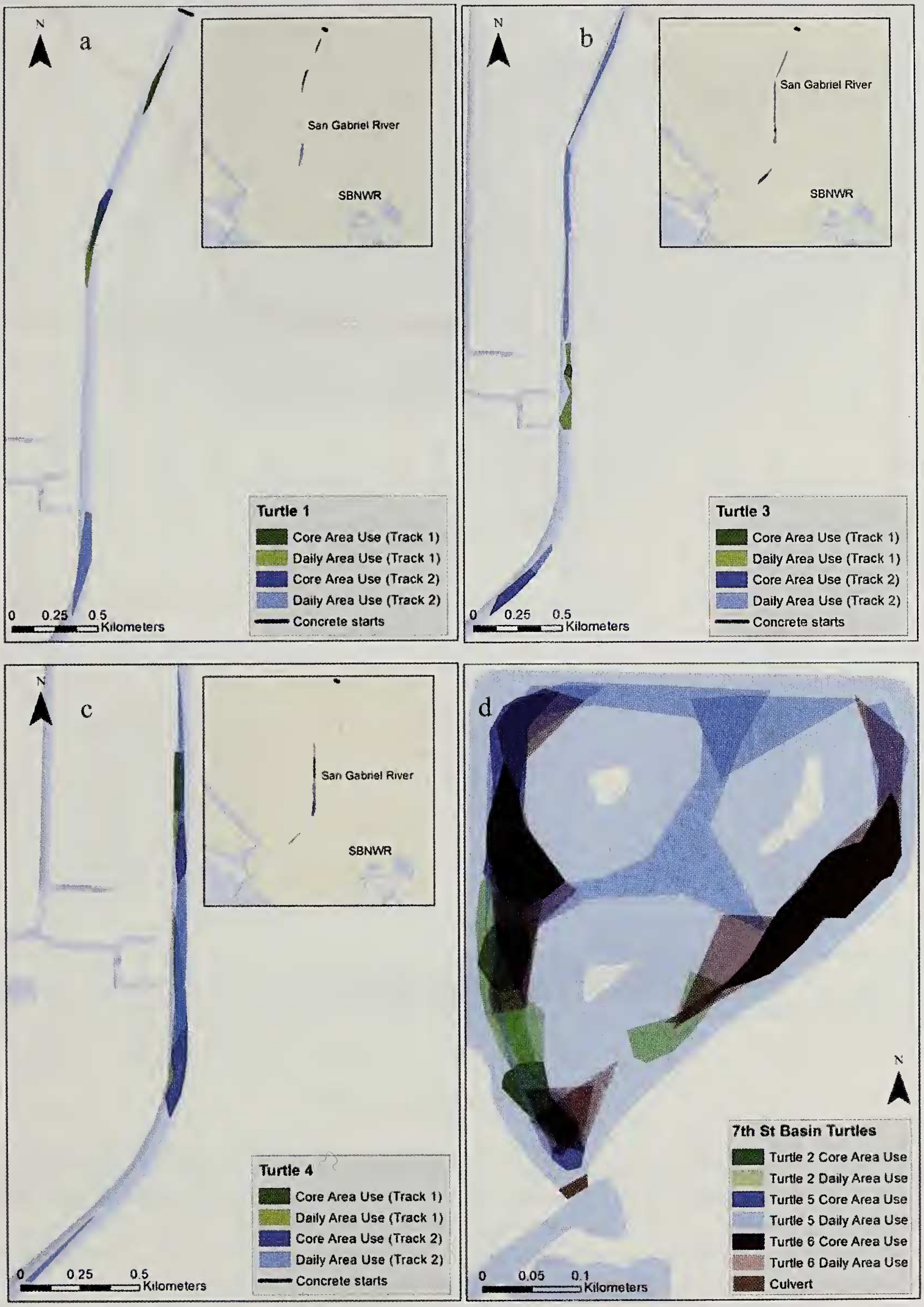

Fig. 2. Core areas and daily areas created by LoCoHs of both tracks of (a) Turtle 1, (b) Turtle 3, and (c) Turtle 4 in the San Gabriel River and (d) both tracks of Turtles 2, 5, and 6 in the 7th St. Basin. The lightest shade of blue represents the water and the white in the center of the basin represents the three islands.

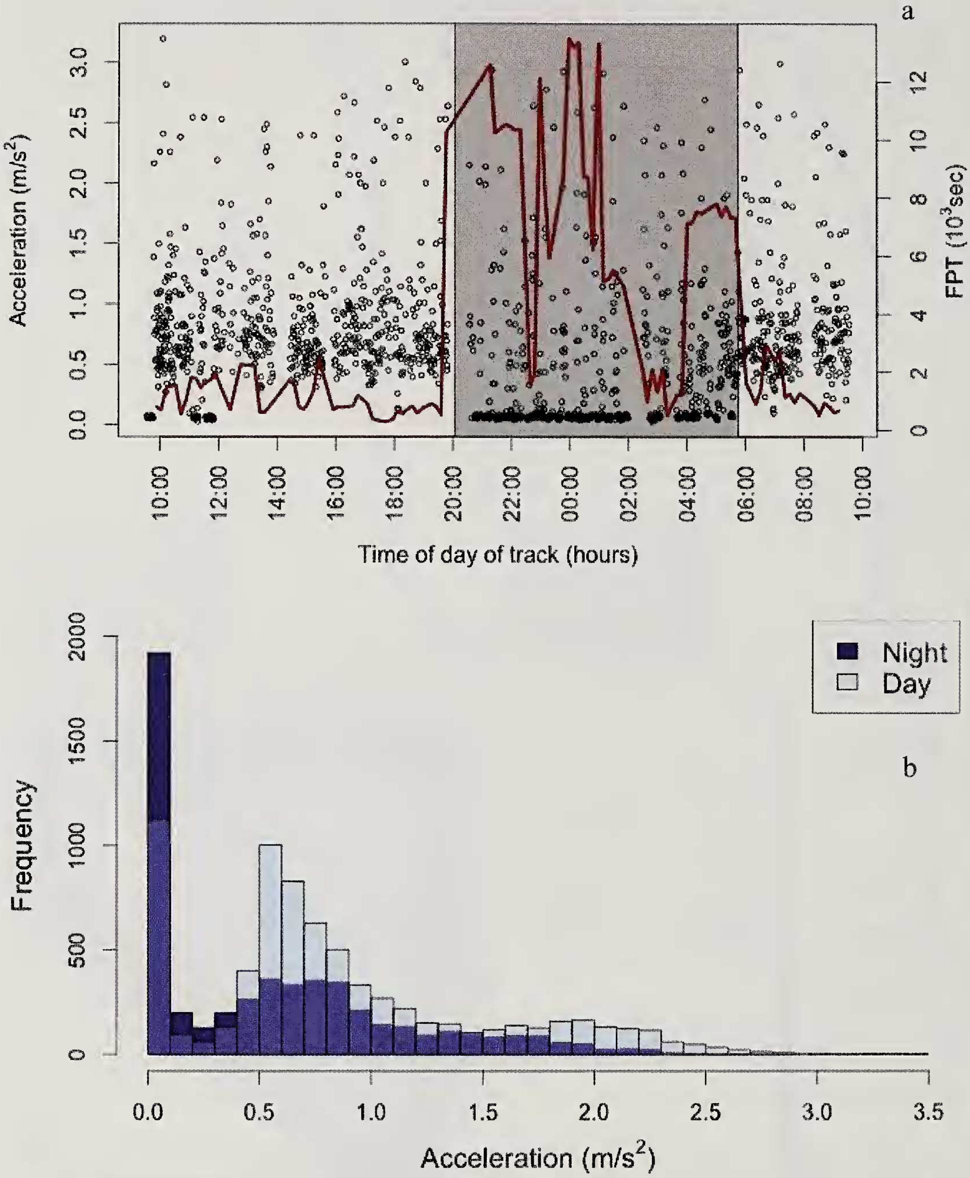

Fig. 3. (a) Raw acceleration (circles) values from the second track of Turtle 2 overlaid by FPT (red line) values. The grey box represents the period between sunset and sunrise on the date of the track. (b) Distribution of all acceleration values during the night and day for Turtle 7 monitored for 69 days by the acoustic array in the San Gabriel River. The middle blue shade indicates where the two histograms overlap.

significant difference in distance traveled (ANOVA, $F_{1,4} = 0.14$, $p = 0.73$) or ROM (ANOVA, $F_{1,4} = 0.10$, $p = 0.77$) for turtles tracked between sites (Table 3).

Actively tracked turtles had unique habitat preferences within both sites. However, turtles only appeared to show a diel difference in HSI at one habitat type (culvert/eelgrass in the 7th St. Basin: day: 0.67 ± 0.04; night: 2.62 ± 1.34); therefore, only 24-h HSI was used for each track. In the river, green turtles exhibited the greatest mean HSI and highest selection for

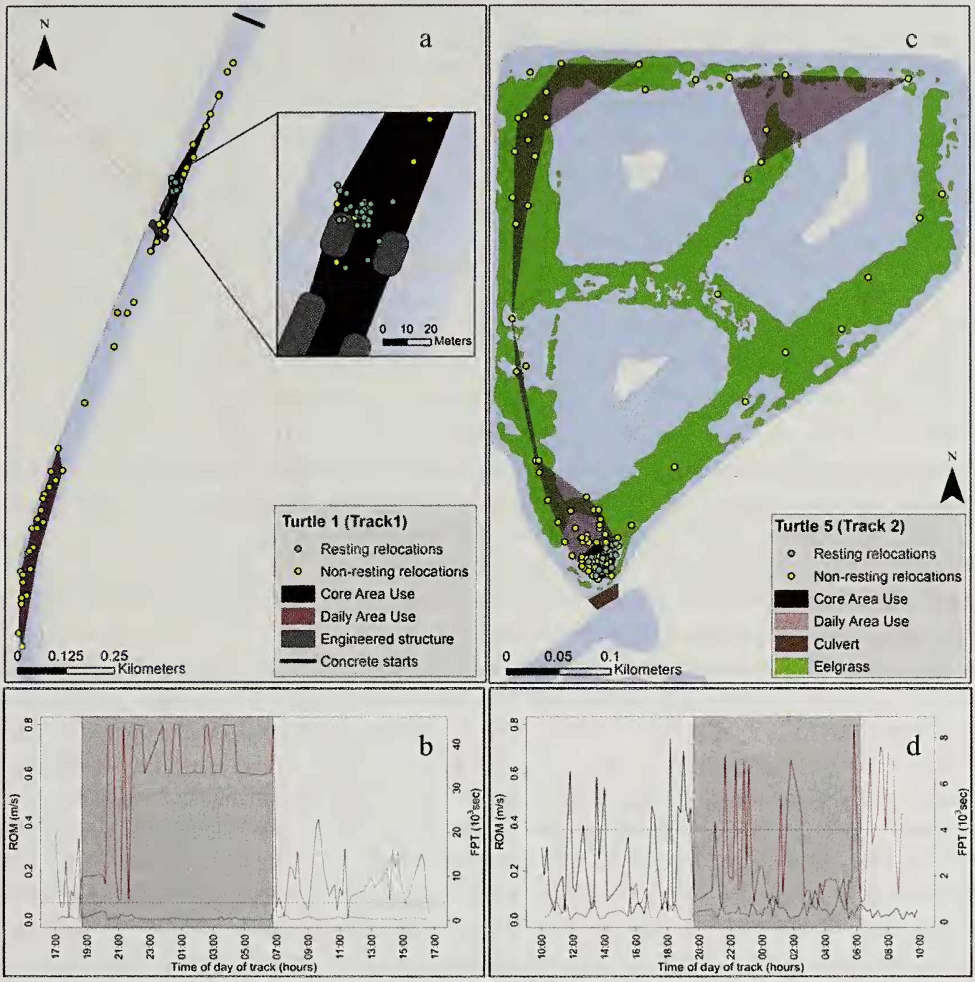

Fig. 4. (a) Resting and non-resting geolocations of the first track of Turtle 1 in the San Gabriel River with an enlarged inset of the area where resting occurred and (c) second track of Turtle 5 in the 7th St. Basin. Plots represent the ROM (black line) and FPT (red line) values against the time of day of (b) the first track of Turtle 1 and (d) second track of Turtle 5. The blue dashed line represents the 4000 second threshold, where FPT values greater than 4000 seconds indicates periods of resting.

engineered structures (2.99 ± 0.76), followed by non-vegetated substratum (1.11 ± 0.04), while not selecting for mixed rubble/soft substratum (0.63 ± 0.24) and hard rubble (0.29 ± 0.08) (Chi-squared test, $\chi^2 = 149.09$, $p < 0.001$). While resting in the river, turtles selected areas associated with engineered structures (3.56 ± 0.33) followed by non-vegetated substratum (1.06 ± 0.05), while not selecting for hard rubble (0.35 ± 0.29) and mixed rubble/soft substratum (0.32 ± 0.32) (Chi-squared test, $\chi^2 = 57.34$, $p < 0.001$; Fig. 4a). In the 7th St. Basin, green turtles displayed the greatest mean HSI and highest selection for culvert/non-vegetated (6.10 ± 3.14), followed by culvert/eelgrass (1.57 ± 0.61) and no culvert/eelgrass (1.36 ± 0.19), while not selecting for no culvert/non-vegetated (0.44 ± 0.10) (Chi-squared test, $\chi^2 = 919.09$, $p < 0.001$). While resting in the basin, turtles selected areas associated most often with culvert/non-vegetated (11.59 ± 9.24), followed by culvert/eelgrass (2.34 ± 1.58) and no culvert/eelgrass

Table 3. Mean and standard error of rate of movement (ROM) and distance traveled for the six active tracks at each site during the day, night and 24-h periods. SGR = San Gabriel River

Metric	Site	Day	Night	24 hours
ROM	SGR	0.15 ± 0.008	0.06 ± 0.006	0.11 ± 0.005
(m/s)	7th St. Basin	0.12 ± 0.006	0.06 ± 0.004	0.09 ± 0.004
Distance Traveled	SGR	6.29 ± 3.73	2.22 ± 0.79	8.51 ± 1.43
(km)	7th St. Basin	4.67 ± 0.77	2.42 ± 0.70	7.08 ± 0.95

(1.28 ± 0.70), while not selecting for no culvert/non-vegetated (0.18 ± 0.13) (Chi-squared test, $\chi^2 = 564.12$, $p < 0.001$; Fig. 4c).

Discussion

This study is the first study to look at green turtle habitat use at this fine of scale (10 min intervals) for a continuous 24-hs, particularly within an urbanized habitat. In addition, by coupling both horizontal movements and activity we were able to more accurately infer behavior (i.e. resting) than is typically possible using a single data source (e.g. dive profiles). This study is also one of the few studies that have directly compared habitat use and behavior between two very different habitats (urbanized river vs. restored estuary).

We identified how green turtles behave and use habitat in an urban environment (i.e. the San Gabriel River) compared to a more "natural" environment (i.e. SBNWR). Despite insignificant differences in the distance traveled, ROM, and core area size between sites, all metrics were all higher in the river. Additionally, there still was a significantly larger daily area use in the river, which suggests that the prey abundance within the river may be patchier and less abundant, while prey abundance (i.e. eelgrass) in the 7th St. Basin may be higher and more concentrated. The presence of eelgrass, which typically offer high primary and secondary productivity and supports an abundance and diversity of invertebrates (Beck et al. 2001) is found among restored estuaries along southern California (i.e. SBNWR and Bolsa Chica Ecological Reserve); however, due to the major anthropogenically-induced shifts in habitat structure in the San Gabriel River, eelgrass is not present. The lack of eelgrass may require turtles to search more area for sufficient nutritional prey items like mobile invertebrates (Lemons et al. 2011) leading to less tortuous movements (Papastamatiou et al. 2011, Ahr et al. 2015) and larger daily area use in the river (Makowski et al. 2006, Seminoff and Jones 2006). It has been shown that in response to habitat features, green turtles have an opportunistic feeding strategy where they have a combined diet (Amorocho and Reina 2008). Although the contribution of river flow to the net flow downriver is often low (with the exception of during rain events), tidal fluxes and power plant discharge can lead to variation in net flow downriver. Therefore, river velocity may also influence turtle movements (i.e. higher flow rate may result in less tortuous movements; Brooks et al. 2009). Lastly, the shape difference between the two sites should not affect tortuous movements because the widths were similar between the river and the basin (Fig. 1).

Despite the lack of eelgrass in the river, the higher number of green turtles occupying the river year round compared to the 7th St. Basin (Crear et al. 2016) suggests that they are able to exploit other resources (i.e. invertebrates and algae) in the river. In fact, a higher abundance of individuals may lead to an increase in search area, which is also supported by a larger daily area use and the lack of overlap of core areas among different individuals and between tracks of the same individual in the river. If resources are being used in a specific area (a different turtle's core area), then a turtle may need to expand its search area (daily area) and find a different location (core area) that has resources it can exploit. The lack of overlap among individuals' core and daily areas may also be driven by seasonal temperature differences in the river, which is a major factor that influences the long term movements of green turtles in the San Gabriel River (Crear et al. 2016). For example, Crear et al. (2016) found that green turtles in the San Gabriel River used more of the river during the spring and fall months compared to during the winter and summer months. During the more extreme temperature seasons (i.e. winter and summer), temperature may constrain the area use of many turtles to certain parts of the river, which would lead to area use overlap among individuals. Further, seasonality influences prey density, which may impact green turtle area use. For example, it was clear that algae concentration was more dense during the warmer months in both locations.

Resting behavior occurred primarily at night at both sites, a pattern observed in green turtles in other studies (Mendonca 1983, Taquet et al. 2006, Hazel et al. 2009) and suggests that the urbanized environment within the San Gabriel River may not alter the natural resting behavior of green turtles. Typically if individuals feed during the day, they might use periods at night to digest food and rest. Turtles that exhibited periods of resting during the day may have had two feeding bouts during the day, one in the morning and one in the afternoon, with a digestive resting period midday, which is a behavior previously observed in green turtles in the U.S. Virgin Islands (Ogden et al. 1983). Despite, the slight differences in resting behavior among individuals and low sample size, this study found similar results as previous literature suggests. Individuals that did not undergo resting over a 24-h period may have been foraging or searching for prey. Where we could correlate horizontal with acceleration data to predict periods of resting (Hart et al. 2016), we were unable to use this method to identify periods of foraging as turtle foraging behavior consists of more precise movements that cannot be identified through acoustic telemetry.

Green turtles were able to exploit some of the urbanized features within the San Gabriel River (bridge pilings and discharge outflows) as seen by a high affinity to these types of structured habitats while resting, compared to low relief substrates. Similar to other reef ledges, engineered structures offer ledges and outcroppings that can provide suitable resting sites for green turtles that block the net flow downriver (Shaver 1994, Brill et al. 1995, Makowski et al. 2006, Hazel et al. 2013). Turtles were also selecting for this habitat type during the day. Hard structures offer areas where a high abundance of invertebrates and algae can attach; therefore, turtles may be exploiting engineered structures along the side of the river to feed during the day. Similarly, Renaud et al. (1995) found green turtles feeding on algae along jetties. Further, turtles have also been observed using vertical features to self or symbiotically clean (Thomson et al. 2015), another behavior these individuals may undergo along engineered structures.

Despite the more "natural" environment within the SBNWR, green turtles showed a high affinity to the culvert within the 7th St. Basin. Similar to engineered structures in the San Gabriel River, the culvert offers attachment sites for invertebrates and algae. Further, the incoming tide and warm temperature may bring small fish and invertebrates into the 7th St. Basin. This potential food source may have drawn green turtles to the culvert opening during the day. In addition, the incoming and outgoing tide through the culvert scours out the bottom (Jirik and Lowe 2012), creating a slightly deeper habitat at the basin's entrance. While resting, green turtles selected areas adjacent to the culvert, which provides deeper habitat and may result in an increase in the duration of resting dives (Hart et al. 2016). This behavior occurs because at deeper depths, turtles need to take a big breath in order to obtain neutral buoyancy at the bottom. This allows for a longer resting time because there is more available oxygen for physiological processes, which minimizes expected energy expenditure (Minamikawa et al. 1997, Hays et al. 2004). This has been observed in green and loggerhead turtles, *Caretta caretta*, where that as dive depth increased, dive duration increased as well in suspected resting dives (Minamikawa et al. 1997, Hart et al. 2016). Seeking out the deepest depth allows them to attain neutral buoyancy on the bottom, while maximizing the oxygen stored in their lungs (Minamikawa et al. 1997, Hays et al. 2004).

Conclusions

The urbanized San Gabriel River that has rocky edges and no eelgrass offers a very different habitat for green turtles than the more "natural" restored 7^{th} St. Basin that has a single culvert and an abundance of eelgrass. Despite the differences in habitat, green turtles seem to exploit the available resources, particularly those associated with manmade structures, at each site. Although periods of foraging could not be identified using our methods, the use of both sites for multiple 24-h periods by all actively tracked turtles suggests that they offer important foraging habitats that support green turtles. The ability for green turtles to undergo typical behavior for multiple 24-h periods in the absence of eelgrass and the presence of manmade structures within the San Gabriel River, suggests that green turtles may be able to adapt and use habitats in certain urbanized environments. Despite the low sample size, we can still provide managers with what may be expected in the future as more individuals move into these types of environments. As green turtle populations continue to increase and the ocean temperatures warm, we may see an increase in the abundance of individuals at their northern range, leading to range expansion and an increase in individuals settling in these highly developed regions. Therefore, as mitigation projects continue along the coastline, it may be beneficial for managers to consider species that may be able to utilize areas that humans have altered (Seney and Landry Jr 2008). Despite restoration efforts, humans are still heavily influencing coastal habitats; therefore, understanding how a recovering threatened species behaves in these altered and restored environments will help ensure populations continue to increase.

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Literature Cited

Ahr B., M. Farris and C.G. Lowe. 2015. Habitat selection and utilization of white croaker (*Genyonemus lineatus*) in the Los Angeles and Long Beach Harbors and the development of predictive habitat use models. Mar. Environ. Res. 108:1–13.

Allen, A.O. and J.J. Feddema. 1996. Wetland loss and substitution by the Section 404 permit program in southern California, USA. Environ. Manage. 20:263–274.

Amorocho, D. F. and R.D. Reina. 2008. Intake passage time, digesta composition and digestibility in East Pacific green turtles (*Chelonia mydas agassizii*) at Gorgona National Park, Colombian Pacific. J. Exp. Mar. Bio. Ecol. 360:117–124.

Balazs, G., R. Miya and S. Beavers. 1996. Procedures to attach a satellite transmitter to the carapace of an adult green turtle, Chelonia mydas. NOAA Technical Memorandum NMFS-SEFSC. 387:21–26.

Balazs, G. H. and Chaloupka M. 2004. Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. Biol Conserv. 117:491–498.

Bates, D., Maechler M., Bolker B. and Walker S. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.

Beck, M.W., K.L. Heck Jr., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B.Halpern, C.G. Hays, K. Hoshino and T.J. Minello 2001. The Identification, conservation, and manage ment of estuarine and marine nurseries for fish and invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51:633–641.

Bivand, R. and N. Lewin-Koh. 2013. maptools: Tools for reading and handling spatial objects. R package version 0.8-27. http://cran.r-project.org/package=maptools.

Blumenthal, J.M., T.J. Austin, J.B. Bothwell, A.C. Broderick, G. Ebanks-Petrie, J.R. Olynik, M.F. Orr, J.L. Solomon, M.J. Witt and B.J. Godley. 2010. Life in (and out of) the lagoon: fine-scale movements of green turtles tracked using time-depth recorders. Aquat. Biol. 9:113–121.

Brill, R.W., G.H. Balazs, K.N. Holland, R.K.C. Chang, S. Sullivan and J.C. George. 1995. Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L.) within a foraging area in the Hawaiian islands. J. Exp. Mar. Bio. Ecol. 185:203–218.

Brooks, L.B., J.T. Harvey and W.J. Nichols. 2009. Tidal movements of East Pacific green turtle *Chelonia mydas* at a foraging area in Baja California Sur, México. Mar. Ecol. Prog. Ser. 386:263–274.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197:516–519.

Carrión-Cortez, J.A., P. Zárate and J.A. Seminoff. 2010. Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. J. Mar. Biol. Assoc. UK 90:1005–1013.

Chaloupka, M. and C. Limpus. 2001. Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. Biol. Conserv. 102:235–249.

Crear, D.P., D.D. Lawson, J.A. Seminoff, T. Eguchi, R.A. LeRoux and C.G. Lowe. 2016. Seasonal shifts in the movement and distribution of green sea turtles *Chelonia mydas* in response to anthropogenically altered water temperatures. Mar. Ecol. Prog. Ser. 548:219–232.

Fauchald, P. and T. Tveraa 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84:282–288.

Furrer, R., D. Nychka and S. Sain. 2013. fields: Tools for spatial data. R package version 6.8. :http://cran.r-project.org/package=fields.

Getz, W.M., S. Fortmann-Roe, P.C. Cross, A.J. Lyons, S.J. Ryan and C.C. Wilmers. 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS ONE 2:207.

Getz, W.M. and C.C. Wilmers 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27:489–505.

Godley, B.J., A.C. Broderick and G.C. Hays. 2001. Nesting of green turtles (*Chelonia mydas*) at Ascension Island, South Atlantic. Biol. Conserv. 97:151–158.

Goshe, L.R., L.Avens, F.S. Scharf and A.L. Southwood. 2010. Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology. Mar. Biol. 157:1725–1740.

Hart, K.M., C.F. White, A.R. Iverson and N. Whitney. 2016. Trading shallow safety for deep sleep: juvenile green turtles select deeper resting sites as they grow. Endanger. Species Res. 31:61–73.

Hays, G.C., J.D. Metcalfe and A.W. Walne. 2004. The implications of lung-regulated buoyancy control for dive depth and duration. Ecology 85:1137–1145.

Hazel, J., M. Hamann and I.R. Lawler. 2013. Home range of immature green turtles tracked at an offshore tropical reef using automated passive acoustic technology. Mar. Biol. 160:1–11.

Hazel, J., I.R. Lawler and M. Hamann. 2009. Diving at the shallow end: green turtle behaviour in near-shore foraging habitat. J. Exp. Mar. Bio. Ecol. 371:84–92.

Heithaus, M.R., J.J. McLash, A. Frid, L.M. Dill and G.J. Marshall. 2002. Novel insights into green sea turtle behaviour using animal-borne video cameras. J. Mar .Bio.l Assoc. UK. 82:1049–1050.

Jirik, K.E. and C.G.Lowe. 2012. An elasmobranch maternity ward: female round stingrays, *Urobatis halleri*, use warm, restored estuarine habitat during gestation. J. Fish. Biol. 80:1227–1245.

Lemons, G., R. Lewison, L. Komoroske, A.Gaos, C.T. Lai, P. Dutton, T. Eguchi, R. LeRoux and J.A. Seminoff. 2011. Trophic ecology of green sea turtles in a highly urbanized bay: insights from stable isotopes and mixing models. J. Exp. Mar. Bio. Ecol. 405:25–32.

MacDonald, B.D., R.L. Lewison, S.V. Madrak, J.A. Seminoff and T. Eguchi. 2012. Home ranges of East Pacific green turtles *Chelonia mydas* in a highly urbanized temperate foraging ground. Mar. Ecol. Prog. Ser.

461:211–221.

MacDonald, B.D., S.V. Madrak, R.L. Lewison, J.A. Seminoff and T. Eguchi. 2013. Fine scale diel movement of the east Pacific green turtle, *Chelonia mydas*, in a highly urbanized foraging environment. J. Exp. Mar. Bio. Ecol. 443:56–64.

Makowski, C., J.A. Seminoff and M. Salmon. 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. Mar. Biol. 148:1167–1179.

Mendonca, M.T. 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Copeia. 1013–1023.

Minamikawa, S., Y. Naito and I. Uchida. 1997. Buoyancy control in diving behavior of the loggerhead turtle, Caretta caretta. J. Ethol. 15:109–118.

Musick, J. and C. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. Pp. 137–163 in The Biology of Sea Turtles (P. Lutz and J. Musick, eds.) CRC Press.

O'Brien, J.W., H.K. Hansen and M.E. Stephens. 2011. Status of fishes in the Upper San Gabriel River Basin, Los Angeles County, California. Calif. Fish and Game. 97:149–163.

O'Toole, A., K. Murchie, C. Pullen, K. Hanson, C. Suski, A. Danylchuk and S. Cooke. 2011. Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. Mar. Freshwater Res. 61:1446–1456.

Ogden, J.C., L. Robinson, K. Whitlock, H. Daganhardt and R. Cebula 1983. Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. J. Exp. Mar. Bio. Ecol. 66:199–205.

Papastamatiou, Y.P., D.P. Cartamil, C.G. Lowe, C.G. Meyer, B.M. Wetherbee and K.N. Holland. 2011. Scales of orientation, directed walks and movement path structure in sharks. J. Anim. Ecol. 80:864–874.

Papastamatiou, Y.P., P.A. DeSalles and D.J. McCauley. 2012. Area-restricted searching by manta rays and their response to spatial scale in lagoon habitats. Mar. Ecol. Prog. Ser. 456:233.

Pinheiro, J., D. Bates, S. DebRoy and D. Sarkar. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–111.

Renaud, M.L., J.A. Carpenter and J.A. Williams. 1995. Activities ofjuvenile green turtles, *Chelonia mydas*, at a jettied pass in south Texas. Fish. Bull. 93:586–593.

Seminoff, J.A., T. Jones and G.J. Marshall. 2006. Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? Mar. Ecol. Prog. Ser. 322:269–280.

Seminoff, J.A. and T.T. Jones. 2006. Diel movements and activity ranges of green turtle (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. Herpetol. Conserv. Biol. 1:81–86.

Seminoff, J.A., A. Resendiz and W.J. Nichols. 2002a. Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Mar. Ecol. Prog. Ser. 242:253–265.

Seminoff, J.A., A. Resendiz, W.J. Nichols, T.T. Jones and C. Guyer 2002b. Growth rates of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. Copeia. 2002:610–617.

Seney, E.E. and A.M. Landry Jr. 2008. Movements of Kemp's ridley sea turtles nesting on the upper Texas coast: implications for management. Endanger. Species Res. 4:73–84.

Shaver, D.J. 1994. Relative abundance, temporal patterns, and growth of sea turtles at the Mansfield Channel, Texas. J. Herpetol. 491–497.

Smith, J.B. 1999. Western wetlands: the backwater of wetlands regulation. Nat. Resour. J. 39:357.

Taquet, C., M. Taquet, T. Dempster, M. Soria, S. Ciccione, D. Roos and L. Dagorn. 2006. Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. Mar. Ecol. Prog. Ser. 306:295–302.

Thomson, J.A., A. Gulick and M.R. Heithaus. 2015. Intraspecific behavioral dynamics in a green turtle *Chelonia mydas* foraging aggregation. Mar. Ecol. Prog. Ser. 532:243–256.

Topping, D., C. Lowe and J. Caselle. 2005. Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. Mar. Biol. 147:301–311

Turner, C.H. and A.R. Strachan. 1969. The marine environment in the vicinity of the San Gabriel River mouth. California Fish and Game 55:53–68.

Whiting, S.D. and J.D. Miller. 1998. Short term foraging ranges of adult green turtles (*Chelonia mydas*). J. Herpetol. 330–337.